THE GENERA OF LYTHRACEAE IN THE SOUTHEASTERN UNITED STATES [1]

SHIRLEY A. GRAHAM

LYTHRACEAE Jaume St.-Hilaire, Expos. Fam. **2:** 175. 1805, "Lythrariae," nom. cons.

(LOOSESTRIFE FAMILY)

Herbs or shrubs [rarely small trees], with quadrangulate or terete stems. Leaves opposite, seldom alternate or whorled, simple, entire, exstipulate. Flowers regular or irregular, axillary or in terminal racemes or spikes, sometimes dimorphic or trimorphic with regard to style and stamen length, bisexual, [3]4–6-merous, with perianth and stamens perigynous, the flowers rarely cleistogamous; bracteoles 2, opposite on the pedicel, rarely none. Floral tube campanulate to tubular, persistent, often conspicuously nerved; calyx lobes 4–6, alternating with 3–5 deltoid appendages, or the appendages wanting. Petals 0–6, distinct, crumpled, deciduous [rarely persistent], inserted on the inner surface of the floral tube between the calyx lobes. Stamens as many as or twice as many as the petals [or more numerous], often alternately unequal, inserted on the inner surface of the floral tube below the petals, included to exserted; anthers versatile [rarely basifixed], introrse, 2-locular, longitudinally dehiscent. Gynoecium syncarpous, often surrounded at the base by a hypogynous disc, or in irregular flowers the disc on the upper (adaxial) side only; stigma capitate, rarely bilobed; style filiform; ovary superior, free in the floral tube, 2–4[–6]-locular, the septa complete or reduced; placentation axile [rarely parietal]; ovules anatropous and epitropous, with 2 integuments. Fruit a membranaceous [or leathery] capsule inclosed by the persistent floral tube, septicidally or loculicidally dehiscent or indehiscent, splitting irregularly. Seeds 3 to many, minute or up to ca. 4 mm. long, pyramidal, ovoid, or discoid, sometimes slightly winged, with

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Gray Herbarium and the Arnold Arboretum made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Reed C. Rollins and Carroll E. Wood, Jr. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. **39:** 296–346. 1958). The area covered in this, as in former treatments, is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. Material included in the descriptions in brackets applies to species outside this area, and references marked by an asterisk have not been seen by the author.

The aid of Dr. Wood and the observations and suggestions of Drs. H. E. Ahles, R. K. Godfrey, D. B. Ward, and C. A. Brown are gratefully acknowledged. Dr. R. B. Channell kindly supplied living material of *Cuphea* for study.

little or no endosperm; embryo straight with a short radicle, the cotyledons flat [rarely convolute], often auriculate-cordate. Embryo sac development of the normal (Polygonum) type (rarely intermediate between Polygonum and Oenothera type); endosperm development of the nuclear type. (Salicariae Juss., 1789.) TYPE GENUS: *Lythrum* L.

A family of about 24 genera and 450 species, most abundant in the New World tropics and subtropics, but present in temperate to tropical areas of Europe, Asia, Africa, and Australia; six genera represented in our area.

Koehne (1903) divided the family into two tribes based on the condition of the septa in the ovary. In tribe Lythreae the septa are interrupted or split above the placenta, which is then discontinuous with the style; in Nesaeeae Koehne the septa are complete and the placenta is continuous with the style. This character is variable and difficult to ascertain in many specimens. If tribal divisions are to be used at all, a firmer basis for their delimitation is needed.

Similarities in anatomy and embryology closely link the Lythraceae with the Myrtaceae, Onagraceae, Punicaceae, and Sonneratiaceae (see Mauritzon, 1939). The Lythraceae are distinguished from these families by the superior ovary which is free in the floral tube. The family is characterized anatomically by intraxylary phloem which forms bicollateral bundles in the leaves.

Unique, spirally grooved, inverted hairs are found in the epidermal layer of the seed coat in several genera (e.g., *Cuphea*, *Peplis*, and some species of *Lythrum*). Upon contact with water, the hairs emerge through the outer wall of an epidermal cell and slowly uncoil to a length of two or three millimeters. The hairs are slightly mucilaginous and may serve in dispersal by attaching the seed to passing objects.

Heteromorphism is widespread in the family. *Lythrum*, *Decodon*, and *Nesaea* have species with trimorphic flowers, and species with dimorphic flowers are known in *Lythrum, Rotala*, *Pemphis*, and *Nesaea*. Cleistogamous flowers have been reported in *Ammannia* and are thought to occur in the apetalous species of *Rotala*, *Peplis*, and *Nesaea*.

Fossil remains of the Lythraceae are known from the Eocene through the Pleistocene. At least six genera of fossil seeds belonging to the Lythraceae have been described. All are well suited to aquatic dispersal by means of winglike expansions of the seed coat and/or buoyant spongy tissue on the outer seed coat. The aquatic or semiaquatic habit of many Lythraceae is undoubtedly an ancient characteristic, still present, but less prevalent in modern species.

Two genera, *Lawsonia* and *Lagerstroemia*, are cultivated in warm-temperate and tropical regions of the world. *Lawsonia inermis* L., native to northeastern Africa, is the henna of commerce, yielding an orange-red dye which has been used for centuries in the Near and Far East for coloring the hair, fingernails, and soles of the feet. The leaves contain hydroxynaphthaquinone which reacts directly with the keratin of human hair and skin to form the bright pigment.

The crape-myrtle, *Lagerstroemia indica* L., $2n = 48, 50$, a native of Asia, is a very popular shrub or tree widely cultivated throughout our southern states. It is showy in bloom, producing great numbers of magenta flowers. A number of horticultural varieties bearing purple, pink, or white flowers are planted. The trees are long lived and may persist where planted long after dwellings have disappeared. For this reason, they may appear to be naturalized but are usually only remnants of cultivation and not true escapes. One possible exception is the presence of several young plants in the sparsely inhabited sand-hill country of Berkeley County, South Carolina (*H. E. Ahles 52982*, NCU). Collectors of this species should note the circumstances under which the plants are growing and record any evidence of reproduction from seed.

REFERENCES:

BAILLON, H. Lythrariacées. Hist. Pl. **6**: 426–457. 1877.

BENTHAM, G., & J. D. HOOKER. Lythrarieae. Gen. Pl. **1**: 773–785. 1867.

CANDOLLE, A. P. DE. Lythrarieae. Prodr. **3**: 75–94. 1828.

COPELAND, E. B. Daily growth movements of *Lagerstroemia*. Philip. Jour. Sci. Bot. **8**: 287–298. 1913.

DILLON, C. B. The hundred days' flower. A brief history of the crepe myrtle. La. Conserv. Rev. **6**(1): 21–23, 25. 1937.

GIN, A. Recherches sur les Lythracées. Trav. Lab. Mat. Méd. Paris **6**: 1–166. 1909.*

GÜNTHER, W. . . . Beiträge zur anatomie der Myrtifloren mit besonderer Berücksichtigung der Lythraceae . . . Inaug.-diss. 39 pp. Universität Breslau. 1905.*

HARRIS, J. A. Variation and correlation in the flowers of *Lagerstroemia indica*. Missouri Bot. Gard. Rep. **20**: 97–104. 1909.

———. On a chemical peculiarity of the dimorphic anthers of *Lagerstroemia indica*, with a suggestion as to its ecological significance. Ann. Bot. **28**: 499–507. 1914. [Suggests presence of a chemical substance in the yellow, but not the red, anthers which keeps the pollen moist, so it can be readily gathered by insect visitors.]

JOSHI, A. C. Embryological evidence for the relationships of the Lythraceae and related families. Curr. Sci. Bangalore **8**: 112, 113. 1939.* [Lythraceae and allied families not closely related to Caryophyllaceae.]

——— & J. VENKATESWARLU. Embryological studies in the Lythraceae. I–III. Proc. Indian Acad. Sci. B. **2**: 481–493, 523, 524. 1935. (See also *ibid.* **3**: 377–400. 1936.*) [*Lawsonia* and *Lagerstroemia* investigated.]

KOEHNE, E. The Lythraceae of the United States. Bot. Gaz. **10**: 269–277. *pl. 6*. 1885.

———. Lythraceae. Pflanzenreich IV. **216**(Heft 17): 1–326. 1903.

———. Lythraceae. Nachträge. Bot. Jahrb. **41**(2): 74–110. 1907; *ibid.* **42**(2, 3): 47–53. 1909.

MAURITZON, J. Zur Embryologie einiger Lythraceen. Acta Horti Gothob. **9**: 1–21. 1934.

———. Contributions to the embryology of the orders Rosales and Myrtales. Lunds Univ. Årsskr. II. Sect. 2. **35**: 1–121. 1939. [Lythraceae, 64–68.]

REDGROVE, H. S. The cultivation and uses of henna. Gard. Chron. III. **85**: 13, 14. 1929.

SAHNI, B. Indian silicified plants. 2. *Enigmocarpon parijai*, a silicified fruit from the Deccan, with a review of the fossil history of the Lythraceae. Proc. Indian Acad. Sci. B. **17**: 59–96. 1943.

SCHOCH-BODMER, H., F. BUXBAUM, & W. WANGERIN. Lythraceae. *In*: O. KIRCHNER, E. LOEW, & C. SCHRÖTER, Lebensgeschichte der Blütenpflanzen Mitteleuropas. **3**(5): 1–128. 1937. [Includes extensive bibliography.]

SPRAGUE, T. A., & C. R. METCALFE. The taxonomic position of *Rhynchocalyx*. Kew Bull. **1937**: 392–394. 1937. [Closely related to *Lawsonia* and wrongly excluded from the Lythraceae by Koehne.]

KEY TO THE GENERA OF LYTHRACEAE

General characters: *Leaves entire, mostly opposite; floral tube campanulate to cylindrical, persistent; ovary superior, free in the floral tube; petals crumpled; fruit capsular; seeds without endosperm, the embryo straight.*

A. Floral tube campanulate to globose, about as long as wide.
  B. Plant woody, perennial, over 1 m. tall.
    C. Flowers in axillary dichasia; stamens 8–10; shrubs of shallow water. ..... 1. *Decodon.*
    C. Flowers in terminal panicles; stamens numerous, more than 10; terrestrial trees or shrubs. ..... [*Lagerstroemia.*]
  B. Plant herbaceous, annual, generally less than 50 cm. tall.
    D. Appendages in the sinuses of the calyx lobes present; capsule dehiscent; flowers 1 to many in the axils of leaves; petals 4 (rarely 0).
      E. Middle and upper leaves attenuate at base; capsule dehiscing septicidally, the outer wall of capsule finely and densely striate; flowers solitary in the axils of leaves. ..... 2. *Rotala.*
      E. Middle and upper leaves cordate to auriculate at base; capsule dehiscing irregularly, the outer wall of the capsule smooth, not striate; flowers (1–)3 to many in the axils of leaves. ..... 3. *Ammannia.*
    D. Appendages in the sinuses of the calyx lobes none; capsule indehiscent; flowers solitary in the axils of leaves; petals 0. 4. *Peplis.*

A. Floral tube cylindrical, elongate, about twice as long as wide.
  F. Flowers regular; floral tube entire in fruit; capsule dehiscing septicidally from the apex, the placenta included; seeds numerous, mostly more than 20. ..... 5. *Lythrum.*
  F. Flowers irregular; floral tube and capsule splitting longitudinally along the upper (adaxial) side in fruit, the placenta then exserted; seeds 3–20. ..... 6. *Cuphea.*

1. Decodon J. F. Gmelin, Linn. Syst. Nat. ed. 13. 2(1): 677. 1791.

Short-lived glabrous or pubescent perennial shrubs or tall herbs of marshy habitats, spreading by means of arching branches rooting at the tips; stems terete to 6-angled, the submerged portions thickened by spongy aerenchyma. Leaves membranaceous to leathery, decussate or verticillate, lanceolate, shortly petiolate, the base and apex acute. Inflorescence of 1–3 shortly pedunculate axillary dichasia at a node, the peduncles partly fused with the petiole. Flowers regular, 4- or 5-merous, trimorphic;

bracteoles 2, ovate to linear, opposite, at the base of the pedicel, early deciduous. Floral tube campanulate, greenish, inconspicuously nerved; calyx lobes 4 or 5(–7), the apex acuminate; appendages narrowly triangular, thickened, mostly twice the length of (rarely equal to) the calyx lobes. Petals 4 or 5(–7), rose-purple, deciduous, about twice the length of the floral tube. Stamens 8–10, deciduous; filaments of 3 possible lengths, two of the three lengths occurring in any one flower and alternating in a single whorl; anthers orbicular in outline. Gynoecium sessile, the disc wanting; stigma capitate; style thin, included to exserted, of 3 possible lengths; ovary 3(4)-locular, the septa complete. Fruit a loculicidally dehiscent capsule. Seeds ca. 20–30, small, inverted-pyramidal with rounded edges, an oval germination valve covered by a spongy epidermal layer present on the adaxial side. TYPE SPECIES: *D. verticillatus* (L.) Ell. (Name from Greek, *deca*, ten, and *odous*, tooth, in reference to the five sepals and five appendages of the floral tube.) — SWAMP LOOSESTRIFE, WATER-OLEANDER, WATER-WILLOW.

A monotypic genus now occurring only in the eastern United States from Louisiana to Florida and north to Minnesota and central Maine. The glabrous var. *laevigatus* Torr. & Gray has been recognized in the northern part of the range. In the Mio-Pliocene the genus was represented by at least two other species from western Europe and central Russia. Fossil seeds of these suggest they were very closely related, but not identical, to the extant *Decodon verticillatus*. Silicified fruit remains from the Eocene of India may represent either *Decodon* or an extinct genus similar to it.

Extensive aerenchyma is produced in concentric layers on submerged stems. The tissue is composed of large thin-walled parenchyma supported by radial columns of cells and by additional strands of elongated cells which obliquely cross several layers to strengthen the tissue. The meristem which produces aerenchyma develops in a narrow zone of parenchyma between the phloem fibers and sieve tube area. Some species of *Ammannia* and *Lythrum* in aquatic situations also develop aerenchyma, but to a lesser degree than in *Decodon*.

Endlicher subordinated *Decodon* to a section of *Nesaea*, but most subsequent authors have regarded it as distinct.

REFERENCES:

Under family references see KOEHNE (1885, 1903).

KOEHNE, E. Ueber Inflorescenz und Trimorphismus von *Decodon* (*Nesaea*) *verticillatus*, einer nordamerikanischen Lythracee. Verh. Bot. Ver. Brandenb. **16**: 42, 43. 1874.

NIKITIN, P. A. The systematic position of the fossil genus *Diclidocarya* E. M. Reid. (With a note by Mrs. E. M. Reid.) Jour. Bot. **67**: 33–38. *pl. 589*. 1929. [Two of three spp. = *Decodon*.]

SCHRENK, J. On the floating tissue of *Nesaea verticillata* (L.) H.B.K. Bull. Torrey Bot. Club **16**: 315–323. *pls. 95–97*. 1889.

2. **Rotala** Linnaeus, Mant. Pl. Alt. 175. 1771.

Annual [rarely perennial], glabrous herbs of aquatic or marshy habitats. Leaves membranaceous, decussate, verticillate, or alternate, linear to oblanceolate [to ovate], attenuate to the base, sessile to short petioled. Flowers regular, solitary and axillary [or in terminal spikes], [3]4–6-merous, [seldom dimorphic,] sessile, with 2 opposite bracteoles at the base of the floral tube. Floral tube campanulate to globose or urceolate, 2.5–5 mm. long, greenish; calyx lobes 4[–6], the apex acute to acuminate; appendages shorter than to exceeding the lobes [or wanting]. Petals [0 or] 4[–6], white or pink, small, scarcely exceeding the calyx lobes, deciduous [rarely persistent]. Stamens 4[–6], included [to exserted]. Gynoecium without a disc at the proximal end; stigma capitate; style very short or wanting; ovary incompletely 3- or 4[–6]-locular, the upper portion of each septum ± incomplete. Fruit a membranaceous, septicidally dehiscent capsule with dense, transverse striations on the outer wall, [2-] 3- or 4-valved. Seeds many, minute, ovoid in outline, plano-convex. TYPE SPECIES: *R. verticillaris* L. (Name from Latin, *rota*, wheel, in allusion to the whorled leaves of the type species.) — TOOTH-CUP.

A genus of about 45 species, best represented in Asia and Africa. Of the three North American species, only *Rotala ramosior* (L.) Koehne, $2n = 32$, is present in our area, occurring in all the Southeastern States. The more robust plants occurring inland from the Atlantic Coastal Plain have been recognized as var. *interior* Fern. & Grisc. The species closely resembles *Ammannia* in general habit and was originally described in that genus. Bentham and Hooker considered *Rotala* synonymous with *Ammannia*, but the close resemblance to *Ammannia* is found only in *R. ramosior*; the genera can be distinguished easily on the basis of at least three characters. *Rotala* has solitary axillary flowers, a septicidally dehiscent capsule, and the outer wall of the capsule densely striate, a character present in no other genus of the Lythraceae. In *Ammannia* the flowers occur in axillary cymes, the capsule dehisces irregularly, and the outer wall of the capsule is smooth.

REFERENCES:

Under family references see KOEHNE (1885, 1903).

FERNALD, M. L., & L. GRISCOM. Three days of botanizing in southeastern Virginia. Rhodora **37**: 129–157, 167–189. *pls. 332–351.* 1935. [*R. ramosior* var. *interior*, 169.]

LEWIS, W. H., H. L. STRIPLING, & R. G. ROSS. Chromosome numbers for some angiosperms of the southern United States and Mexico. Rhodora **64**: 147–161. 1962. [*R. ramosior*, 152.]

3. **Ammannia** Linnaeus, Sp. Pl. 1: 119. 1753; Gen. Pl. ed. 5. 55. 1754.

Annual glabrous herbs of aquatic or marshy habitats. Leaves membranaceous, decussate, linear to lanceolate or oblanceolate, sessile, the base cordate to auriculate, rarely attenuate. Flowers regular, 4(5)-merous,

never heteromorphic, in sessile or pedunculate axillary cymes, (1–)3–15 flowers at a node; bracteoles 2, linear, opposite, at the base of the floral tube. Floral tube campanulate to urceolate, becoming globose in fruit, 1.5–6 mm. long, greenish to rose colored, 8-nerved with 4 nerves especially prominent at anthesis; calyx lobes 4 (5), short and broad; appendages thick, shorter than to equaling the calyx lobes [or wanting]. Petals 0–4, small, pink [white], early deciduous. Stamens 4(–8), included to exserted. Gynoecium without a disc at the base; stigma capitate; style thin, longer than the ovary and exserted, or thick, shorter than the ovary and included; ovary incompletely 2–4(5)-locular, the upper portion of the septa ± incomplete. Fruit a membranaceous, irregularly dehiscent capsule, with the outer wall smooth, not striate. Seeds many, minute, ovoid. LECTOTYPE SPECIES: *A. latifolia* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. **2**: 577. 1913. (Named in honor of Paul Ammann, 1634–1691, a German botanist from Leipzig, not Johan Ammann; see Linnaeus, Crit. Bot. 91. 1737.)

A genus of world-wide occurrence, with about 20 species; represented in the southeastern United States by two to four species. *Ammannia coccinea* Rottb. is found throughout the eastern United States, in the western coastal states, and in Mexico, Central America, the Caribbean region, and northern South America. In Mississippi and elsewhere outside our area (e.g., Oklahoma, Missouri, and Indiana), intermediates occur between this and *A. auriculata* Willd., which is generally found west of the Mississippi River. *Ammannia auriculata* differs from *A. coccinea* mainly in having more densely clustered, smaller, long-pedicellate flowers. A third species, *A. teres* Raf., of swamps or fresh to brackish tidal marshes, ranges from New Jersey to Florida, Mississippi, and Texas. In southern Florida it is replaced by *A. latifolia* L., which extends southward through the Antilles into northern South America. The two are distinguished only by the lack of petals in *A. latifolia* and should probably be considered variants of a single species. Cleistogamous flowers have been reported in *A. latifolia*. A re-evaluation of specific limits in the genus is needed.

REFERENCES:

Under family references see KOEHNE (1903) and MAURITZON (1934, 1939).

JONES, F. B. *Ammannia teres* Raf. (Lythraceae) in coastal Texas. Field Lab. **26**: 85. 1958.

JOSHI, A. C., & J. VENKATESWARLU. Structure and development of the synergids in *Ammannia baccifera* Linn. New Phytol. **34**: 144–150. *pl. 3*. 1935. [See also correction, *ibid*. **35**: 92. 1936; developing endosperm wrongly interpreted as syn-synergids.]

4. **Peplis** Linnaeus, Sp. Pl. 1: 332. 1753; Gen. Pl. ed. 5. 154. 1754.

Delicate annual herbs growing along lake margins or submerged in shallow water. Leaves membranaceous, opposite or alternate, sessile, narrowly linear or oblanceolate, the base acute to obtuse. Flowers regular,

4[–6]-merous, solitary, axillary on short pedicels or sessile; bracteoles 0 [or 2, opposite on the pedicel]. Floral tube broadly campanulate [to globose], 2–3 mm. long; calyx lobes 4[–6], the appendages wanting [or long-subulate]. Petals 0 [or 6, but early deciduous]. Stamens (2?) 4[–6], included. Gynoecium without a disc at the base; stigma capitate or slightly bilobed; style very short or wanting; ovary incompletely 2-locular, appearing 1-locular by reduction of the septum. Fruit a membranaceous, indehiscent capsule, splitting irregularly. Seeds many, small, dorsiventrally flattened, spathulate, the distal end slightly enlarged and curved. (Including *Didiplis* Raf.) TYPE SPECIES: *P. Portula* L. (Ancient Greek name applied by Dioscorides to *Euphorbia Peplis* and by Pliny to "porcillaca or purslain," *Portulaca oleracea*.) — WATER-PURSLANE.

A European genus of eight species; represented in the United States by the endemic *Peplis diandra* Nutt. ex DC., which ranges from Florida to eastern Texas, northward to Minnesota, and to North Carolina. This species displays a terrestrial form having cuneate-lanceolate leaves and a short style, and an aquatic form which generally has longer, narrower, linear leaves, shorter internodes, and no style. The specific epithet *diandra* is perhaps misleading, being based on an atypical plant with only two, rather than the normal four, stamens.

The separation of *Peplis diandra* by some authors as *Didiplis diandra* (DC.) Wood has been made on the basis of its four-merous, rather than six-merous, flowers and the lack of appendages on the floral tube. In view of the numerous other shared characters, e.g., irregularly splitting capsules with many seeds, campanulate floral tube, general plant habit, there seems to be no reason for retaining *Didiplis* as distinct from *Peplis*. Koehne considered *Didiplis* synonymous with *Peplis* but circumscribed subg. DIDIPLIS for this one species.

No insect visitors have been reported for the genus. The most widespread European species, *Peplis Portula* L., $2n = 10$, is known to be self-pollinated, and the floral morphology suggests that this is probably the rule for the other species. The stigma is short and in a position to receive pollen from the introrse anthers lying above it in the floral tube, while insect-attracting petals and nectaries are wanting. Cleistogamy is suspected in the apetalous species.

REFERENCES:

Under family references see KOEHNE (1885, 1903).

KOEHNE, E. Genus-Recht der Gattung *Peplis*. Verh. Bot. Ver. Brandenb. **19**: 47–53. 1877.

WILLIS, J. C., & I. H. BURKILL. Flowers and insects in Great Britain. Ann. Bot. **9**: 227–273. 1895. [*P. Portula*, 266.]

5. **Lythrum** Linnaeus, Sp. Pl. 1: 446. 1753; Gen. Pl. ed. 5. 205. 1754.

Annual or perennial herbs or shrubs of moist, often brackish habitats. Leaves membranaceous, decussate, alternate [or verticillate], ovate to

linear [or obovate], sessile or shortly petiolate, the base attenuate to cordate. Flowers regular [or slightly irregular], (4–)6-merous, sometimes heteromorphic with 2 [3] floral forms, the flowers axillary [or in terminal spikes or racemes], 1 or 2 [to several] sessile or shortly pedicellate flowers at a node; bracteoles [0] 2, on the pedicel, linear, opposite. Floral tube cylindrical, greenish, 8–12-nerved, 4–8 mm. long; calyx lobes (4–)6, the apex acute to acuminate, the appendages narrowly triangular, shorter than to exceeding the calyx lobes. Petals (4–)6 [rarely 0], rose-purple or white, deciduous. Stamens (4–)6[–12] in 1 [2] whorls, inserted deep in the floral tube, included to exserted; filaments in heteromorphic forms of 2 [3] lengths. Gynoecium sessile or stipitate, with or without a hypogynous disc at the proximal end; stigma capitate; style thin, included to exserted, in heteromorphic forms of 2 [3] lengths; ovary 2-locular, the septum ± incomplete. Fruit a membranaceous [rarely leathery] capsule, dehiscing septicidally or septifragally. Seeds [8 to] many, small, ovoid in outline. LECTOTYPE SPECIES: *L. Salicaria* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. 2: 580. 1913. (Name from Greek, *lythron*, gore or blood; thought to refer to the purple color of the petals.) — LOOSESTRIFE.

A genus of about 30 species, with its greatest development in North America (ca. 16 species), but also occurring in Europe, Asia, Africa, and Australia. The North American species are badly in need of revision. Past treatments have depended heavily on variable characters of the leaf for delimitation of species. Hybridization among species in different parts of their range is suspected but has not been studied. Understanding of the breeding patterns and morphological variation seems necessary for a more satisfactory treatment of this group.

The genus is represented in our area by six weakly defined species of sect. EUHYSSOPIFOLIA Koehne (plants grayish or bluish-green, calyces mostly tubular, flowers 4–6-merous, petals present). The most common and widespread indigenous *Lythrum* in the eastern United States is *L. lanceolatum* Ell., characterized by appendages exceeding the sepals and alternate, linear to elliptic leaves with tapering bases. Within its range is *L. Curtissii* Fern., reportedly endemic to southwestern Georgia and adjacent Gadsden County, Florida. This species, with slightly smaller flowers, larger stem leaves, and smaller branch leaves than *L. lanceolatum*, probably represents a local variant of *L. lanceolatum*. *Lythrum lineare* L., named for its linear, strictly opposite leaves, is restricted to brackish marshes on or near the coast from New Jersey to Florida, and west along the gulf coast to eastern Texas. Specific lines separating *L. alatum* Pursh, $2n = 10$, *L. dacotanum* Nieuw., and *L. flagellare* Shuttl. ex Chapm. are very tenuous. Misinterpretation of *L. alatum* has increased difficulties in recognizing species within this group (see Shinners).

Several species in North America (including *Lythrum lanceolatum*, *L. lineare*, and *L. alatum*) have two floral forms, an individual having either flowers with long styles and short stamens or short styles with long

stamens. The plants are generally self-sterile and outbreeding. The most successful crosses occur between stamens and styles of corresponding lengths. Pollination is accomplished by insects. The most detailed studies on dimorphic flowers have been conducted on the genus *Primula* (Primulaceae). The dimorphic *Lythra* have not been investigated.

The occurrence of plants having three floral forms was first noted by Vaucher (1841) in *Lythrum Salicaria* L., $2n = 30, 50, 60$, a Eurasian species long naturalized in Canada and the northeastern United States and now occurring southward at least to Virginia. The first extensive account of this phenomenon was given by Darwin (1865). In this species there are three style lengths and three sets of stamens of lengths corresponding to those of the styles. Each floral form has one style length and two whorls of stamens, one whorl for each of the other two possible lengths. The forms are termed long-, mid-, or short-styled, depending on whether the style exceeds, lies between, or is shorter than the two whorls of stamens. An individual plant bears only one of the three floral forms.

Genetically, the long-styled form has been shown to be homozygous and recessive for long styles, while the short-styled form differs from long- and mid-styled by a single epistatic gene. The mid-styled flowers carry duplicate factors for "mid-" in the same linkage group, with the homozygous condition of either or both factors producing a lethal effect.

Pollen differs in color, size, and amount of stored starch in each of the three stamen lengths. The longest stamens have the largest grains, the anthers are green, and the pollen grain is filled with starch. The two shorter stamen lengths have yellow anthers and correspondingly smaller pollen containing less starch. The two kinds of pollen in each floral form carry identical hereditary factors for the inheritance of trimorphism. In like manner, the stigmatic papillae vary in length with the length of the style, being longest on the longest style.

The flowers are slightly irregular, with the stigma and anthers bent upward toward the open side of the flower. Insects of several different orders visit the species. They are able to pass only along the open side of the flower to reach the nectar at its base, and, in moving toward the nectaries, their underside brushes both the upturned stigma and the anthers. The pollen is transported on the ventral side of the insect mainly in three places, corresponding to the position of the three stamen lengths, and is consequently transferred to styles of those lengths, effecting cross-pollination.

Crosses occurring between style and stamens of corresponding length are very fertile and are termed "legitimate" unions; conversely, those between style and stamens of unequal length (including self-pollinated flowers) are generally unsuccessful and are termed "illegitimate" unions. Exceptions are the successful crosses obtained between mid-styled plants pollinated by long stamens of the short-styled form and short stamens of the long-styled form. It is probable that pollen from more than one stamen length is dusted onto a style, but studies indicate that unidentified chemical

growth inhibitors present in the style prevent the pollen of illegitimate unions from competing with that of legitimate unions.

Products of most illegitimate crosses are highly sterile, often dwarfed, and rarely persist. Seedlings of mid-styled illegitimate crosses are, however, more hardy and fertile than other illegitimate unions. Darwin found that although the mid-styled form produced seed by illegitimate as well as legitimate unions, the stamens of that form were less fertile than were those corresponding stamens of the other two forms, suggesting that in the mid-styled form there is a tendency toward functional dioecism. All three forms are believed to have been derived from a single homomorphic, self-compatible form. A semihomomorphic form has been reported in which the style and one whorl of stamens are the same length, being intermediate in position between long- and mid-styled forms. It has been suggested that heterostyly is an unstable state in *Lythrum Salicaria*, the presence of an intermediate form and the variable degrees of self-compatibility evidenced by the three floral types tending to support this conclusion. Trimorphism has been reported for only four other genera: *Nesaea* and *Decodon*, of the Lythraceae; *Oxalis*; and a single monocotyledonous genus, *Pontederia*.

Fossil flowers of *Lythrum* have been found in the Lower Pliocene of Japan (see Miki). This determination is based on the flower's being four-sepalate, a rare condition in modern species. Miki also found fossils of *Trapa* and *Hemitrapa* Miki (an extinct genus) and, on the basis of a comparative study, concluded that *Trapa* was derived from *Lythrum* through *Hemitrapa*. Other writers consider Trapaceae closely related to, and perhaps derived from, Onagraceae.

Chromosome numbers of $2n = 10$, 20, 30, 50, and 60 have been reported for the genus, but only one count has been published for the indigenous American species.

REFERENCES:

Under family references see KOEHNE (1885, 1903).

ARARATIAN, A. G. Observations on heterogeny in *Lythrum Salicaria*. (In Russian.) Akad. Nauk Armian. SSR. Dokl. **23**(4): 187–192. 1956.*

BARLOW, N. Inheritance of the three forms in trimorphic species. Jour. Genet. **13**: 133–146. 1923. [*Oxalis valdiviana* and *L. Salicaria*.]

BODMER, H. Beiträge zur Anatomie und Physiologie von *Lythrum Salicaria*.] Beih. Bot. Centralbl. **45**: 1–58. 1928.

DARWIN, C. On the sexual relations of the three forms of *Lythrum Salicaria*. Jour. Linn. Soc. Bot. **8**: 169–196. 1865.

———. The different forms of flowers on plants of the same species. xx + 352 pp. London. 1892.

EAST, E. M. The inheritance of heterostyly in *Lythrum Salicaria*. Genetics **12**: 393–414. 1927. [See also Proc. Natl. Acad. Sci. **13**: 122–124. 1927.]

———. Further observations on *Lythrum Salicaria*. Genetics **17**: 327–334. 1932.

FERNALD, M. L. Some little-known plants from Florida and Georgia. Bot. Gaz. **33**: 154–157. 1902. [*L. Curtissii*, sp. nov.]

FISHER, R. A. On the selective consequences of East's (1927) theory of heterostylism in *Lythrum*. Jour. Genet. **30:** 369–382. 1935.

——— & V. C. MARTIN. Spontaneous occurrence in *Lythrum Salicaria* of plants duplex for the short-style gene. Nature **160:** 541. 1947.

——— & K. MATHER. Polyploid inheritance in *Lythrum Salicaria*. Nature **150:** 430. 1942.

FYFE, V. C. Double reduction at the *mid* locus in *Lythrum Salicaria*. Heredity **7:** 285–292. 1953.

KOSTOFF, D. Pollen-tube growth in *Lythrum Salicaria*. Proc. Natl. Acad. Sci. **13:** 253–255. 1927.

LEHMANN, E. Keimungsversuch mit Samen von *Lythrum Salicaria*. Ber. Deutsch. Bot. Ges. **42:** 55–60. 1925. [Effects of varying light and temperature on seed germination.]

MIKI, S. Evolution of *Trapa* from ancestral *Lythrum* through *Hemitrapa*. Proc. Japan Acad. **35**(6): 289–294. 1959.

MÜLLER, H. Fertilisation of flowers. (Transl. by D. W. Thompson.) xii + 669 pp. London. 1883. [List of insect visitors to *L. Salicaria*, 255, 256.]

RAO, L. Quantitative Untersuchungen über die Wirkung des Lichtes auf die Samenkeimung von *Lythrum Salicaria*. Jahrb. Wiss. Bot. **64:** 249–280. 1925.

SCHOCH-BODMER, H. The influence of nutrition upon pollen grain size in *Lythrum Salicaria*. Jour. Genet. **40:** 393–402. 1940.

———. Pollenbeschaffenheit und fertilität bei *Lythrum Salicaria* L. Bull. Soc. Bot. Suisse **52:** 317–352. 1942.

SCHOUTE, J. C. Ueber die Morphologie der Heterostylie, insbesondere bei *Lythrum Salicaria*. Rec. Trav. Bot. Néerl. **25A:** 271–340. 1928.

SHINNERS, L. H. Synopsis of the United States species of *Lythrum* (Lythraceae). Field Lab. **21:** 80–89. 1953.

SOUÈGES, R. Embryogénie des Lythracées. Développement de l'embryon chez le *Lythrum Salicaria* L. Compt. Rend. Acad. Sci. Paris **180:** 1417, 1418. 1925.

STEVENS, N. E. Observations on heterostylous plants. Bot. Gaz. **53:** 277–308. *pls. 21–23.* 1912. [Extensive bibliography.]

STIRLING, J. Studies of flowering in heterostyled and allied species. II. The Lythraceae: *Lythrum Salicaria* Linn. Publ. Hartley Bot. Lab. Liverpool **10:** 1–24. 1935; III. Gentianaceae, Lythraceae, Oxalidaceae. *Ibid.* **15:** 1–24. 1936.

STOUT, A. B. Studies of *Lythrum Salicaria*. I. The efficiency of self-pollination. Am. Jour. Bot. **10:** 440–449. 1923; II. A new form of flower in this species. Bull. Torrey Bot. Club **52:** 81–85. 1925.

TATEBE, T. Physiological studies on the fertilization in *Lythrum Salicaria* Linn. I. Presence of pollen-germination inhibitors in the ovary. Bot. Mag. Tokyo **74:** 291–295. 1961.

TISCHLER, G. Über die Entwicklung und phylogenetische Bedeutung des Embryosackes von *Lythrum Salicaria*. Ber. Deutsch. Bot. Ges. **35:** 233–246. 1917. [Lythraceae related embryologically to Onagraceae.]

———. Untersuchungen über den anatomischen Bau der Staubund Fruchtblätter bei *Lythrum Salicaria* mit Beziehung auf das "Illegitimitatsproblem." Flora **111/112:** 162–193. 1918.

VAUCHER, J. P. Histoire physiologique des plantes d'Europe **2:** 371. 1841.* [First published reference to tristyly; observed in *L. Salicaria*.]

6. **Cuphea** P. Browne, Civ. Nat. Hist. Jamaica 216. 1756.

Herbaceous or woody annuals or short-lived perennials, mostly with viscid, glandular hairs on stem, leaves, and flowers. Leaves membranaceous [or leathery], decussate or verticillate [rarely alternate], ovate to lanceolate, elliptic or linear, sessile or petiolate. Flowers irregular, 6-merous, homomorphic, sessile or pedicellate, 1–3 at a node: when alternate on the stem one flower at each node interaxillary, the others, if present, axillary; when opposite or verticillate on the stem all flowers interaxillary and often internodal; bracteoles 2, opposite, on the pedicel. Floral tube cylindrical, 4–10[–25] mm. long, green or purple, distinctly 12-nerved, the base gibbous or distinctly spurred, the spur curving downward toward [or upward away from] the pedicel; calyx lobes 6, deltoid, acute to acuminate [rarely apiculate] at apex, equal in size or the upper (adaxial) one larger than the others; appendages shorter than [to exceeding] the length of the calyx lobes. Petals 6 [4, 2, or 0], pale to deep purple, equal in size or the upper (adaxial) 2 or the lower (abaxial) 4 largest, early deciduous [rarely persistent]. Stamens (5–)11(–12), included to exserted, alternately unequal, the filaments often covered with dense hairs, the 2 upper (adaxial) stamens inserted deeper in the calyx tube than the others; pollen triangular or orbicular in outline in polar view, [2]3-colporate, the exine striate. Gynoecium with a disc at the base on the upper side only and free from the side of the ovary; stigma capitate, seldom bilobed; style included or exserted; ovary incompletely 2-locular, appearing 1-locular by reduction of the septum to 2 thin threads, the lower (abaxial) locule smaller, sometimes sterile. Fruit a membranaceous, loculicidally dehiscent capsule, splitting longitudinally the length of the adaxial wall of the ovary, the upper (adaxial) side of the persistent floral tube also splitting, the placenta projecting up and out of the capsule and floral tube. Seeds 3–20[–numerous], orbicular to ovoid in outline, dorsiventrally flattened [rarely not flattened], the surface pebbled, dark brown [mottled green and brown, or light brown], often narrowly margined; cotyledons flattened, cordate to auriculate; radicle short. (*Parsonsia* P. Br.) TYPE SPECIES: *C. decandra* Ait. (*C. ciliata* (Sw.) Koehne, 1881, not *C. ciliata* Ruiz & Pav., 1798). (Name from Greek, *kuphos*, hump, referring to the gibbous or spurred floral tube.)

A genus of 200–250 species, in 13 sections, mostly restricted to the American tropics and subtropics; represented in our area by four species in three sections. The sections are very weakly delimited, and discovery of new species and accumulation of knowledge of variability in the species have further lessened their validity. The entire genus is in need of revision, with emphasis on a more natural arrangement of the species.

The most common species of our area is the annual *Cuphea viscosissima* Jacq. (*C. petiolata* (L.) Koehne, 1881, not *C. petiolata* Pohl ex Koehne, 1877), tarweed or blue waxweed, an endemic to the United States, which ranges from northern Alabama and Georgia and western North and South

Carolina, to central Arkansas, and northward to easternmost Kansas and Massachusetts. Reportedly a bad weed in pastures, old fields and gardens, it is avoided by livestock because of its dense, sticky, glandular hairs. It is most closely related to species of western and central Mexico. A second indigenous species, *C. aspera* Chapm. (*Parsonsia lythroides* Small), with opposite flowers, whorled leaves, pale-purple petals, and tuberous roots, is known only from the immediate vicinity of Port St. Joe, Florida. It is most closely related to *C. hyssopoides* St.-Hil., of Brazil.

The South American *Cuphea glutinosa* Cham. & Schlecht. was first collected in the United States in 1884, in Vermilion Parish, Louisiana, a general area to which it has remained restricted. The petals are characteristically very early deciduous. The presence of *C. carthagenensis* (Jacq.) Macbr. (*C. balsamona* Cham. & Schlecht.) along our coast from Louisiana to North Carolina often has been overlooked. It has been confused with the common *C. viscosissima*, in spite of its distinct geographical range and very different morphology (floral tube green *vs.* purple and green, 4.5–6 mm. *vs.* 8–10 mm. long, petals equal in size *vs.* upper (adaxial) petals largest, and stamens deeply *vs.* shallowly inserted in the tube). The species is native to South America but has spread as far west as the Fiji and Philippine islands and is undoubtedly a relatively recent introduction to the United States. Most early collections are misidentified as *C. viscosissima*. A showy-flowered Mexican species, *C. procumbens* Cav., has been reported from the Blue Ridge, North Carolina, and Andover and Springfield, Massachusetts. These plants were most likely garden escapes which would not have persisted. There is no evidence that the species is established in the eastern United States today.

The genus is morphologically the most highly specialized in the family. It is well adapted to insect and hummingbird pollination by virtue of the long, irregular floral tube, the loss of a stamen in the honey entrance, and the introrsely directed anthers. Glandular-viscid bristles on the floral tube and stems discourage crawling insects from entering the flower, while a disc at the base of the flower narrows the passage to the nectar secreted by the walls of the spur, excluding all but long-tongued insects. Most species are apparently self-compatible but require an insect vector to accomplish pollination. The seeds emerge from the capsule and floral tube while green and remain on the placenta, exposed to the air, for a ripening period.

The interaxillary position of the flowers of *Cuphea* is unique in the family. In the alternate-flowered species, a vegetative bud is present in the axil of one leaf and a floral bud in the axil of the other. The vegetative bud may produce a flowering branch (sometimes highly reduced), or remain suppressed; the floral bud produces a single flower, the pedicel of which traverses and is fused with the internode above, the flower emerging just below or at the node above, between the leaves. In opposite-flowered species, both flowers at the node are interaxillary.

Pollen morphology differs among some species and in these cases provides a useful taxonomic character. One fossil pollen grain of *Cuphea* is known from the Miocene of Alabama. It is three-colporate but does not

belong to any of the species present in the United States today. According to Erdtman, *Cuphea* is isolated from the other genera of the family on the basis of pollen morphology.

Embryologically, *Cuphea* is quite distinct from *Ammannia*, *Nesaea*, *Rotala*, *Peplis*, and *Lythrum*. Its relationship to other genera in the family has not been investigated. Chromosome numbers of $2n = 12$, 16, 18, 20, 24, 32, 36, 72, and ca. 84 have been found in the genus (Graham, unpublished). No counts have been reported for the species in our area.

A few species are cultivated; the best known are *Cuphea platycentra* Lem. (*C. ignea* A. DC.) and *C. procumbens* Cav., commonly called cigar or firecracker plants, after the long, purple or red floral tube.

REFERENCES:

Under family references see KOEHNE (1885, 1903) and MAURITZON (1934, 1939).

AHLES, H. E., C. R. BELL, & A. E. RADFORD. Species new to the flora of North or South Carolina. Rhodora **60**: 10–32. 1958. [*C. carthagenensis*, 19.]

ARDAO, M. I. Contribución al estudio de la *Cuphea glutinosa* Cham. & Schlechtd. y breve noticia de la Litráceas Uruguayas. I. Litráceas del Uruguay; II. Estudio botanico-quimico y farmacodinemico de la *Cuphea glutinosa* Cham. y Schlechtd. Arch. Soc. Biol. Montevideo **8**: 173–201. 1938.

BACIGALUPI, R. Taxonomic studies in *Cuphea*. Contr. Gray Herb. **95**: 1–26. *pls. 1–5*. 1931.

BARCIANU, D. P. Ueber die Blüthenentwicklung der Cupheen. Mitt. Gesammt. Bot. **2**: 179–193. *pl. 11*. 1875.

BAUM, H., & W. LEINFELLNER. Die Plazenta des dorsiventralen *Cuphea*-Gynözeums. Österr. Bot. Zeitschr. **98**: 187–205. 1951. [Correctly interpret the lower (abaxial) locule as reduced, contrary to Koehne's view that it is the upper (adaxial) locule which is reduced.]

BOUBIER, A. M. Recherches anatomiques sur l'inflorescence des *Cuphea* alterniflores (Lythrariées). Bull. Herb. Boiss. **4**: 328–335. 1896.

CORRENS, C. Ueber die Epidermis der Samen von *Cuphea viscosissima*. Ber. Deutsch. Bot. Ges. **10**: 143–152. *pl. 8*. 1892.

DUNCAN, W. H. Stamen-numbers in *Cuphea*. Rhodora **52**: 185–188. 1950. [*C. viscosissima*.]

FOGG, J. M. Weeds of lawn and garden. vii + 215 pp. Philadelphia. 1945. [*C. viscosissima*, 126.]

GRAHAM, S. A. Systematic studies in the genus *Cuphea* (Lythraceae). vi + 235 pp. Ph.D. diss. (unpublished). Univ. Mich. 1963.

GUIGNARD, M. L. Recherches sur le sac embryonnaire des phanérogames angiospermes. Ann. Sci. Nat. Bot. VI. **13**: 136–199. *pls. 3–7*. 1882.

GUTTERSON, M. E. *Cuphea procumbens* at Andover, Massachusetts. Rhodora **4**: 247, 248. 1902.

KERNER, A. Die Schutzmittel der Blüthen gegen unberufene Gäste. Festschr. Zool.-Bot. Ges. Wien. 189–261. *pls. 1–3*. 1876.

KLEBS, G. Beiträge zur Morphologie und Biologie der Keimung. Unters. Bot. Inst. Tübingen **1**: 536–635. 1885. [Discussion of hairs in seed coat of *Cuphea*, 583–585.]

KOEHNE, E. Berichtigung der von D. P. Barcianu gemachten Angaben über

Blüthenentwickelung bei den Cupheen. Bot. Zeit. **33:** 291–296, 302–307. 1875.

MERRILL, E. D. The generic name *Parsonsia* and the status of *Parsonsia helicandra* Hooker and Arnott. Brittonia **1:** 233–237. 1933 [*Parsonia* R. Br., 1810, conserved for a genus of Apocynaceae.]

———. Los nombres *Parsonsia* y *Cuphea*. Revista Sudam. Bot. **1:** 97–99. 1934.

SAITO, K. Studies on inducing polyploid flower plants and their utilization. III. On several polyploid plants of *Cacalia*, *Cosmos*, *Cuphea*, and others. (In Japanese; English summary.) Jour. Hort. Assoc. Japan **19:** 195–199. 1950.* [Colchicine treatment.]